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Abstract: Path integration enables desert ants to return to their nest on a direct path. However, the mechanism of path integration is error prone and the ants often miss the exact position of the nest entrance in which case they engage in systematic search behavior. The pattern produced by this search behavior is very flexible and enables the ants to take the errors into account that have been accumulated during foraging and homing. Here, we assess which parameter the desert ant Cataglyphis fortis uses to adapt its systematic search behavior to the uncertainty of its path integrator when deprived of additional external cues. We compared groups of ants that had covered the same distance between their nest and a food source but differed in the overall length of their foraging excursions. Our results show that the width of the ants' search density profile depends on the distance the ants have ventured out from the nest, that is, the length of the home vector, but not on the tortuousness of their outbound path, that is, the number of steps made during foraging. This distance value is readily available through the path integrator and obviously sufficient to calibrate the ants' systematic search patterns

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Desert ants use foraging distance to adapt the nest search to the uncertainty of the path integrator

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Path integration enables desert ants to return to their nest on a direct path. However, the mechanism of path integration is error prone and the ants often miss the exact position of the nest entrance in which case they engage in systematic search behavior. The pattern produced by this search behavior is very flexible and enables the ants to take the errors into account that have been accumulated during foraging and homing. Here, we assess which parameter the desert ant *Cataglyphis fortis* uses to adapt its systematic search behavior to the uncertainty of its path integrator when deprived of additional external cues. We compared groups of ants that had covered the same distance between their nest and a food source but differed in the overall length of their foraging excursions. Our results show that the width of the ants' search density profile depends on the distance the ants have ventured out from the nest, that is, the length of the home vector, but not on the tortuousness of their outbound path, that is, the number of steps made during foraging. This distance value is readily available through the path integrator and obviously sufficient to calibrate the ants' systematic search patterns. *Key words:* *Cataglyphis*, density profile, foraging distance, path integrator, systematic search, uncertainty. *[Behav Ecol 21:349–355 (2010)]*

Path integration allows desert ants to return to their nest on a straight and direct path after a long and tortuous foraging excursion (Mittelstaedt H and Mittelstaedt M-L 1982; Wehner 2003, 2009; Wehner and Srinivasan 2003). However, the ants cannot afford to exclusively rely on this navigational tool as it continuously accumulates errors (Müller and Wehner 1988; Merkle and Wehner 2009b): the longer the preceding foraging excursion has been, the larger the error with which the ants have to cope (Merkle et al. 2006). Even after short foraging trips, the overall error added up by the path integrator is so substantial that in most cases, the ants would not manage to find the nest entrance straight away (Müller and Wehner 1988; Merkle et al. 2006). Therefore, it is essential for them to have navigational backup systems available that allow for overcoming the effects of their error-prone path integrator.

Among these backup systems are landmark guidance (Wehner et al. 1996; Collett et al. 1998), surface structure (Merkle 2009), and systematic search behavior (Wehner and Srinivasan 1981; Müller and Wehner 1994). The latter takes a prominent position as it is the final and, in featureless terrain, the only available backup system enabling foragers to effectively deal with the deficiencies of the path integration mechanism (Merkle et al. 2006; Merkle and Wehner 2009a). It has to comply with 2 demands: To ensure that, on the one hand, the nest will be found under any circumstances and, on the other hand, that the nest search is as short as possible to minimize the effects of heat, desiccation stress, and predators. Wehner and Srinivasan (1981) analyzed the systematic search behavior of different *Cataglyphis* species and revealed the underlying principle: From the point where the nest is supposed to be according to the information provided by the path integrator, the individual starts searching by performing loops of ever increasing size. After each loop, the ant returns to the starting point of the search, that is, the nest position as indicated by the path integrator, from where the next loop is commenced. Density plots of the search behavior showed that the distribution is similar to a 2D Gaussian curve: The center, where the nest is most likely to be, is searched with highest intensity, and this intensity decreases the further an ant moves away from that point. In other words, this pattern represents the likeliness to find the nest for each particular spot that is searched. Very similar search patterns to find a target—the nest or a food source—have been described for other ants (Fourcassié and Traniello 1994) as well as for other central-place foraging insects such as desert isopods (Hoffmann 1983a,b) or cockroaches (Durier and Rivault 1999), whereas there is an ongoing debate about whether the flight patterns of honeybees that search for known feeding sites contain segments with Lévy distribution or not (Reynolds, Smith, et al. 2007; Reynolds AM, Smith AD, Reynolds DR 2007; but see also Viswanathan et al. 1999; Edwards et al. 2007; Sims et al. 2007).

More recent studies investigated the adaptiveness of the systematic search behavior in desert ants (Merkle et al. 2006; Merkle and Wehner 2009a) and reported a remarkable flexibility of these search patterns: The animals take into account how far they have traveled and, thus, consider the errors the path integrator has accumulated. Longer foraging excursions result in larger overall errors (Merkle et al. 2006). The ants account for this problem by searching the area where the path integrator indicates the nest entrance less intensely and at the same time by performing wider search loops from the beginning. That is, in this case, the ants rely less on the position

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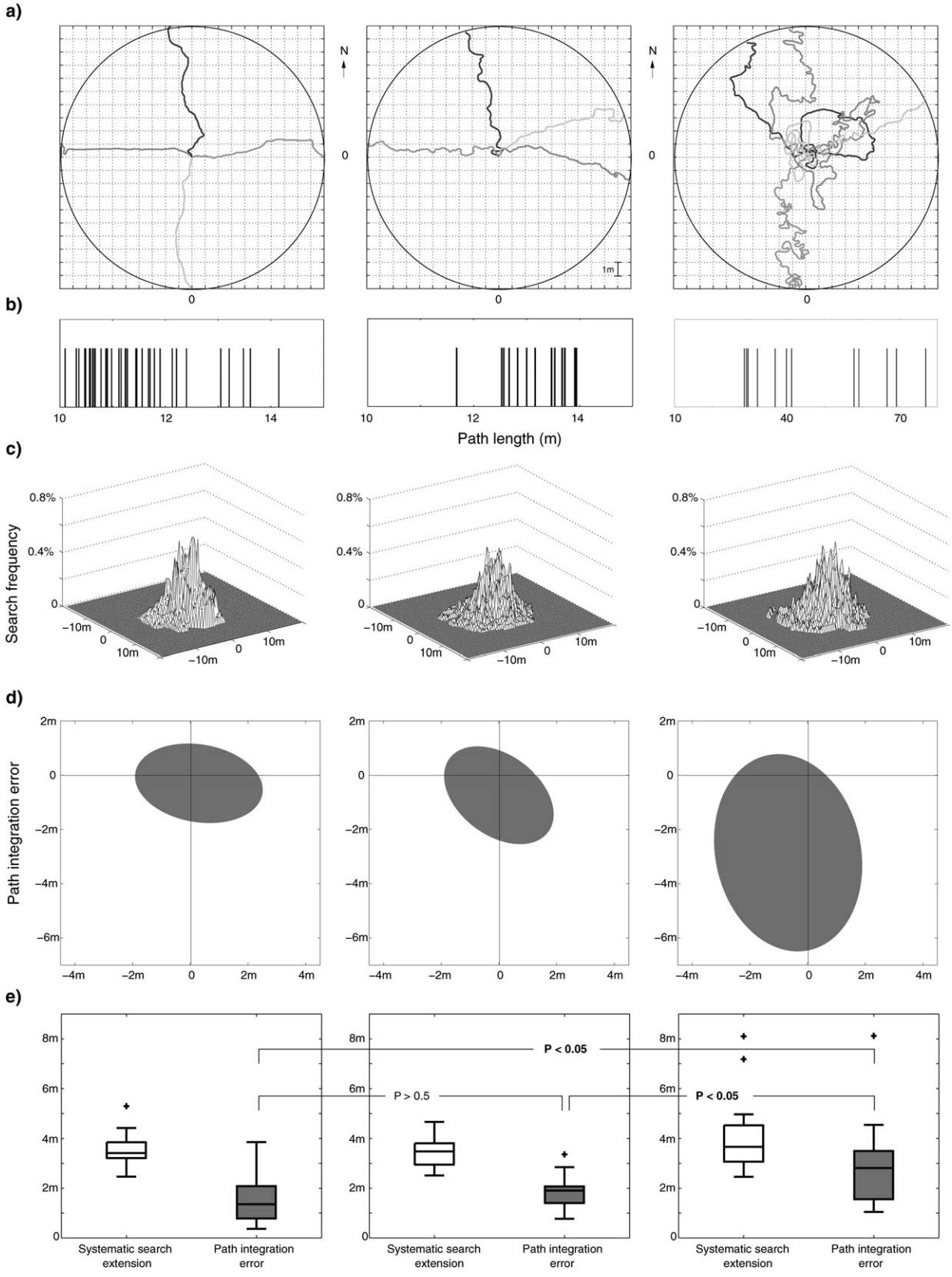

Figure 1
Search density profiles and path integration errors in 3 groups of ants that differ in the length of their outbound paths but coincide in their homing distance (10 m). Left column: trained ants (length of outbound path ≤ 14.15 m), middle column: untrained ants (length of outbound path ≤ 14.15 m), and right column: untrained ants (length of outbound path ≥ 28.30 m). (a) Examples of outbound paths (4 paths per group). Nest position at 0/0. (b) Path lengths of outbound runs; each bar refers to one individual ant. (c) Density plots of the ants' systematic search

provided by the path integrator as compared with shorter foraging excursions. In fact, it is not only the length of the foraging excursion that shapes the systematic search behavior but also certain features of the inbound run such as the distance covered in familiar territory and how close an ant has been to its nest entrance (Merkle and Wehner 2009a).

Here, we address the probably most fundamental question in regards to the systematic search behavior: How exactly do desert ants take the uncertainty of their path integrator into account, and what determines the extension of the systematic search? Because the ants cannot measure the errors of the path integrator directly, they have to rely on other parameters to calibrate their search patterns. They could either use the overall path length (i.e., the number of steps; see Wittlinger et al. 2006) or use the length of the home vector (i.e., the distance between food source and nest). The result of a previous study (Merkle et al. 2006) does not allow for distinguishing between these 2 hypotheses. The current study aims at finally answering this question: We compared the systematic search patterns of groups of ants that had covered the same distance between nest and food source (i.e., the length of their home vectors was identical) but differed in the overall length of their foraging excursions (i.e., the number of steps made during foraging and homing).

Using a novel approach, we recorded the natural trajectories of untrained outbound ants in an open environment. The foragers differed in their overall path lengths but were captured at the same outbound distance from the nest. We compared the systematic search patterns of the 2 most extreme groups, that is, the ants with the longest and the shortest overall path lengths. In addition, we trained ants to feeders at that particular distance from the nest at which ants of the former 2 groups were captured. This last group was also included in the analysis and compared against the 2 other groups. If the overall path length determined the systematic search, we would expect different search patterns in the 3 groups; however, if only the outbound distance mattered, the search patterns should be similar in all 3 groups.

This recording of natural outbound runs also allowed us to analyze whether the overall path integration error increases with increasing length of the foraging run. In similar previous studies, the ants had been trained to food sources, so that the foraging distance and the overall foraging path length were almost identical (Sommer and Wehner 2004; Merkle et al. 2006). We therefore used our data set of natural paths to assess differences in the path integration errors in the 3 groups.

MATERIALS AND METHODS

Study site and species

We conducted this experiment with *Cataglyphis fortis* Forel 1902 at our field station in a salt pan near Maharès, Southern Tunisia (34°32′N, 10°32′E), from June to September 2004. All ants observed in this study belonged to the same nest that was situated in a landmark-free area. The ants of this nest were not involved in any other experiments during the field season 2004. Both wind speeds and temperatures were fairly constant throughout the experiment.

A white grid that had the nest entrance as its center (size 24×24 m, square size 1 m^2) and a circle (radius 10 m, also centered in the position of the nest entrance) were painted on the desert ground (Figure 1a). We kept the area around the nest free of food items throughout the experimental procedures. In order to avoid the observer representing a landmark, he moved continuously and always kept a distance of at least 3 m from the nest entrance. We never detected an influence of the experimenter's position, if the experimenter moves at a distance of 2–3 m to the left, to the right, or behind the animal and if he/she changes his/her position arbitrarily during a homebound run performed by an ant in the test field (Merkle T and Wehner R, personal observation). This setup allowed us to observe untrained desert ants during their natural outbound runs and record this data for the first time.

Experimental setup

Untrained ants

We recorded the outbound paths of 130 foraging ants that had not been influenced prior to the experiment on graph paper with an equivalent grid (scale 1:100), starting from when the ants left the nest until they had reached a radial distance of 10 m from the nest, that is, until they crossed the painted circle (Figure 1a, middle and right). Each ant was immediately captured and kept in a dark container while being transferred to a test area that was approximately 150 m away. The 2 areas were separated by a sand mound (0.6 m high). These circumstances made it very unlikely that ants of this nest had ever been to the test area before. This test area also had a white grid (20×20 m, square size 1 m^2) and did not contain any prominent landmarks either. Each ant was released and provided with a biscuit crumb with which it immediately set off to return to its nest. As it was impossible to find the nest in the test area, the ant started searching for it after having run off the previous outbound distance (10 m). We recorded both the home run to the expected nest location and the systematic search on graph paper (see above). Because the ants could not enter the nest, it was possible to monitor each individual's trajectories for deliberately long time periods. The inbound runs and systematic searches of most animals ($n = 100$) were recorded for 10 min, whereas for 30 ants the recording times were between 5 and 10 min. Each ant was tested only once.

Trained ants

The same experimental setup as described above was used to train ants to particular feeders. We established feeders located either 10 m north, east, south, or west of the nest entrance (i.e., on the 10 m circle, Figure 1a left). By training the ants for at least 1 day, we ensured that all individuals tested in the experiment had performed a sufficient number of foraging trips before they were tested (Åkesson and Wehner 2002).

The test procedure for the trained animals was such that outbound runs of 40 ants (10 ants per direction) were recorded and the ants were captured at the 10 m circle, that is, in this case, the location of the feeder. Then, they were transferred

frequencies. Fictive position of the nest at 0/0. (d) Path integration errors displayed by the homing ants in the test area. The ellipses describing the ants' uncertainties about the position of the nest are computed on the basis of the positions of the ants' centers of search and by means of the least-square fitting method. (e) Box plots (including medians, IRs, whiskers, and outliers) depicting the systematic search extensions (white boxes, see "Data analysis" for the procedure applied to determine search extensions) and the path integration errors (gray boxes) of the test groups. The 3 test groups did not differ in their search extensions (Kruskal–Wallis test: $P > 0.6$) but did in their path integration errors (Kruskal–Wallis test: $P < 0.05$). The P values presented for the path integration errors result from the post hoc comparisons (Tukey's post hoc test) between the 3 groups.

to the test area where their paths were recorded for 10 min each.

The testing procedure of untrained animals preceded this training to rule out the possibility that an ant that was considered untrained had been trained before.

Data analysis

The outbound, inbound, and search runs were digitized one by one using a graphics tablet and GEDIT Graphics Editor and Run Analyser (Antonsen 1995). We defined the end point of the inbound run, that is, the switch to the systematic search behavior, by using a criterion that we had established in earlier studies (Merkle et al. 2006; Merkle and Wehner 2008): It was the point at which the overall path direction changed by at least 30° and from which the ant did not revert to its former direction for the following 3 m.

We calculated the outbound path lengths of all untrained and trained ants. The path lengths of outbound runs in the untrained group ranged from 10.68 to 75.65 m ($n = 130$). As expected, all trained ants headed out toward the feeder on very straight paths, such that their path lengths displayed the narrow range from 10.10 to 14.15 m ($n = 39$). One trained ant had to be excluded as it performed several loops before reaching the feeder.

Trained individuals formed one group in the analysis ($n = 39$). The second group included all untrained ants that had shown similarly straight outbound runs as the trained ones, that is, all ants that exhibited outbound path lengths of 14.15 m (i.e., the maximum length for trained ants) or less. Finally, the third group comprised all untrained ants with outbound path lengths of 28.3 m or more. This particular minimum value was chosen to ensure that the outbound run lengths of both untrained groups differed at least by factor 2, such that any effect could be clearly attributed to differences in the outbound path lengths (Merkle et al. 2006). Due to the natural scatter of the data, a factor of less than 2 between groups could disguise differences between them, whereas factor 2 has been shown to uncover potentially meaningful effects on the search patterns.

We cut all search paths at a search length of 100 m and excluded runs that were shorter than 100 m from the analysis. The width of the search distribution was determined for each ant as the median distance from the search center (i.e., the median position of all x and y coordinates) to all positions recorded for this particular search (a measure introduced in Merkle and Wehner 2009a). We repeated this procedure after cutting the search paths at a path length of 50 m and, thus, checked once more for differences in the search patterns' extensions.

In addition, we backed up our analysis by recalculating the search extensions by means of an earlier measure used in Merkle et al. (2006). In this earlier study, we multiplied the most extreme values along both the x and the y axes with each other. This calculation yielded a value that characterized the area covered by the search behavior. We repeated this analysis for the data of the current study after cutting the searches to 100 m.

To test whether the groups differed in their accumulated errors, we determined the deviation of the systematic search center from the correct nest position for each ant using the median search position (see above). As the end point of the home run might be influenced by different factors such as wind (Wolf and Wehner 2005) or the presence of nest mates (Merkle and Wehner 2009a), our measure of the assumed nest position is biologically more plausible. Desert ants generally underestimate the distance to the nest (Sommer and Wehner 2004; Merkle et al. 2006) as a strategy to search in familiar terrain, where the ants can use additional features such as the surface structure to find the nest more easily (Merkle 2009). Hence, we decided to use the search center as a measure of the ants' estimate of the nest position. Search lengths were cut to avoid potential effects of differences in the overall path lengths of the search patterns.

Table 1
Sample sizes and ranges of the outbound path lengths of the 3 experimental groups

		Untrained ants	
	Trained ants Lengths of outbound paths ≤ 14.15 m	Lengths of outbound paths ≤ 14.15 m	Lengths of outbound paths ≥ 28.30 m
Sample size *N*—Search length 100 m	36	13	12
Sample size *N*—Search length 50 m*	39	21	15
Lengths of outbound runs (m)	10.10–14.15	11.68–13.94	28.60–76.90

*The search extensions were recalculated for search lengths of 50 m.

The final sample sizes and ranges of outbound path lengths of all ants in each group are presented in Table 1 and Figure 1b.

The Kruskal–Wallis one-way analysis of variance was applied to check for statistical differences in both path integration errors and systematic search patterns between the 3 groups. Post hoc comparisons were performed using Tukey's post hoc test.

RESULTS

The main goal of our study was to test whether there are differences in the systematic search patterns between the following 3 groups of ants: trained, untrained (short outbound paths), and untrained (long outbound paths) ants.

The search patterns of the 3 test groups differed only marginally when their searches were cut to 100 m (Kruskal–Wallis test chi square = 0.792, $P > 0.6$, Figures 1c,e and 2). Trained ants displayed very similar search extensions (median $m = 3.41$ m, interquartile range [IR] = 3.21–3.85 m) as compared with the untrained ants with rather straight outbound paths ($m = 3.47$ m, IR = 2.94–3.80 m). Although the foragers with very tortuous outbound paths, that is, very long path lengths, spread their searches slightly more ($m = 3.66$ m, IR = 3.06–4.53 m), the difference to the other groups proved not to be significant. Applying this procedure again for search paths of 50 m length confirmed our result: No differences between the groups were found (Kruskal–Wallis test $P > 0.5$).

Using the earlier measure of comparing the areas covered by the search patterns confirmed the above result (Kruskal–Wallis test $P > 0.2$).

In contrast, the same 3 groups differed strongly in the accuracy of their path integrator (Kruskal–Wallis test chi square = 9.105, $P < 0.05$, Figures 1d,e and 2). The post hoc comparisons revealed that the 2 groups with rather straight outbound runs were similar in how far away from the correct nest position they searched with highest intensity (trained ants: $m = 1.34$ m, IR = 0.78–2.10 m; untrained ants with short outbound path lengths: $m = 1.93$ m, IR = 1.39–2.09 m; Tukey's test $P > 0.7$). Untrained ants with path lengths of more than 28.30 m during their foraging trips searched for the nest much further away from the correct position than the

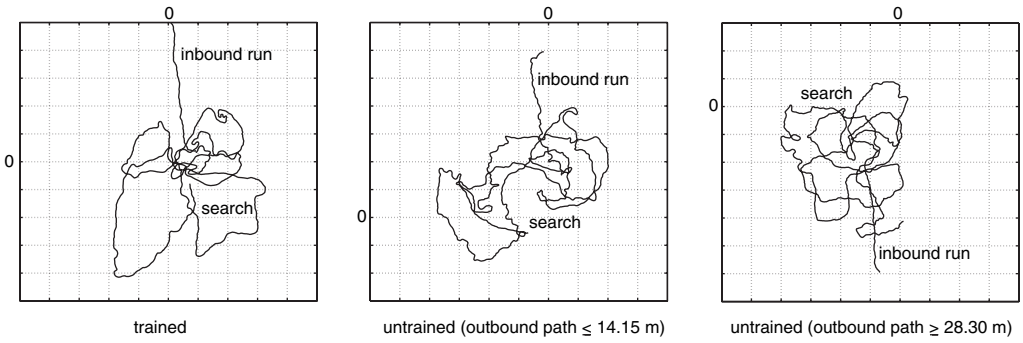

Figure 2
Examples of individual inbound runs and search patterns (100 m) of 3 ants. Left: trained ant (outbound path length ≤ 14.15 m), middle: untrained ant (outbound path length ≤ 14.15 m), and right: untrained ant (outbound path length ≥ 28.30 m). Correct nest position at 0/0.

former 2 groups ($m = 2.80$ m, IR = 1.56–3.50 m; Tukey's test for comparisons with the 2 other groups $P < 0.05$).

DISCUSSION

In this study, we tested how desert ants cope with the uncertainty of navigational errors accumulated by their path integrator and, in particular, how they manage to calibrate their systematic search patterns to the uncertainty associated with the preceding foraging excursion. We compared groups of ants that had covered the same distance during foraging but at the same time varied in their overall outbound path lengths. We captured the ants at a radial distance of 10 m from the nest entrance and then transferred them to an unfamiliar test area, where they reeled off their home vector and searched for the (nonexistent) nest entrance. This experimental procedure eliminated the potential effects of cues acquired during the home run in a familiar area on the systematic search patterns (Merkle and Wehner 2009a). It also ensured that distant landmarks did not have any impact on the search patterns. Consequently, the ants could only memorize the information obtained during their most recent outbound and inbound runs and utilize it for navigating back.

The search patterns of all 3 groups were very similar, irrespective of how long the outbound runs had been. Because the foraging paths of one group (untrained ants with long paths) were at least twice as long as those of the 2 other groups, any potential differences in the search patterns would most likely correlate to the outbound path length (see Merkle et al. 2006). These untrained ants had to deal with larger path integration errors, as predicted by several theoretical path integration models (Mittelstaedt M and Mittelstaedt H-L 1982; Müller and Wehner 1988): The error increases with the length of the foraging run but is not correlated to the maximum distance a forager has ventured out. Based on these findings, the similarity of the search patterns can most conclusively be explained by an underlying calibrating parameter that is the same in all 3 groups and this is the distance between nest and feeder.

This finding raises the tantalizing question: Because the path integration error correlates with the overall path length, why then do ants not shape their search patterns to the length of their outbound path? The systematic search would then be adjusted most accurately: the longer the path and, hence, the larger the accumulated path integration error, the broader the search pattern. This question is all the more viable as we know that ants employ a step integrator to measure distances covered (Wittlinger et al. 2006), and a record of the number of steps made during foraging and homing would suffice to calibrate the searches.

There are at least 2 reasons why using distance proves more useful than path length. First, most foraging runs are rather straight. This becomes obvious by having a closer look at the outbound path lengths of all 130 untrained ants: 77 out of 130 ants (59%) displayed path lengths of less than 20 m and 101 out of 130 ants (78%) of less than 25 m. That is, tortuous outbound runs are more the exception than the rule. Former studies have shown that foragers exhibit high sector fidelity, that is, they keep foraging in areas where they have previously found food (Wehner et al. 1983, 2004; Schmid-Hempel 1984, 1987; see also Wehner 1987 for the foraging patterns of *Cataglyphis albicans*, *Cataglyphis bicolor*, and *C. fortis*). Also, generally, the overall foraging length of an outbound run is correlated with the maximum distance ventured out (Merkle T and Wehner R, unpublished data), such that foraging distance—which the ants store in order to return to profitable food sources (Wehner et al. 1983, 2002; Collett et al. 1999)—is probably an adequate enough value for the adaptation of the systematic search.

Second, despite being able to count their steps, ants do not have the overall length of the foraging path directly available in their path integrator. Although the ants are ready to reel off the home vector at any time (e.g., Müller and Wehner 1988; Merkle and Wehner 2008), that is, they integrate distances and directions continuously, there is no evidence that they also keep track of the total number of steps they have made (e.g., Wehner et al. 1996; Wehner 2003, 2009; Wehner and Srinivasan 2003). It is very plausible that the price to pay for memorizing the number of steps as a separate measure is too high compared with a potential benefit from it. Hence, in terms of physiological constraints, using the outbound distance is the measure of choice.

There are several alternative explanations that could have potentially contributed to the result presented here. We specify them below but also illustrate why—based on previous studies conducted on desert ants—these explanations are unlikely to account for the observed behavior:

For one, foraging experience of individual ants cannot explain our results. Although ants with more tortuous outbound paths were probably less experienced foragers than ants that displayed rather straight paths (Schmid-Hempel 1987), the accuracy of the path integrator has been shown not to improve by repeated foraging trips (Merkle and Wehner 2009b)—neither in experienced nor inexperienced individuals. We can therefore consider foraging experience as unlikely to cause differences in the search patterns.

It could be argued that proximity to the nest during searching might reset the path integrator as foragers with longer and therefore more tortuous outbound runs inevitably approached the nest several times during their runs. We can, however, rule

out the possibility that this influenced their behavior as they would have to enter the nest to reset their path integrator (Collett et al. 2003; Knaden and Wehner 2005).

As the foraging distance of 10 m in our experiment was rather short, it might well be that this study represents a specific case, in particular, because *Cataglyphis* ants have been shown to cover foraging distances of 100 m and more (Wehner R and Wehner S 1990). However, the usual range of recorded foraging distances at our study site is rather low (20–40 m). The fact that we found differences between groups with generally shorter path lengths suggests that these differences might become even more pronounced when analyzing longer foraging distances.

Finally, one alternative explanation for our results is that the ants used experiences from previous runs to calibrate their search patterns. A study conducted by Cheng et al. (2006) proved, however, that *Cataglyphis* relies exclusively on its last outbound run when computing its current home vector. This finding does not necessarily rule out that foragers use previous experiences to adapt their search patterns. However, such a scenario seems very unlikely as memorizing such information for the search alone—and not applying it to the equally important home vector—is certainly contradictory with the efficient way *Cataglyphis* uses its limited memory capacities.

It becomes apparent that desert ants cannot use unlimited memory capacities (Bélisle and Cresswell 1997; Dukas 1999). For instance, *Cataglyphis* foragers do not improve the accuracy of their path integrator while traveling to and fro between the nest and a food site (Merkle and Wehner 2009b). Similarly, they only remember the distance covered during the most recent outbound run (Cheng and Wehner 2002; Cheng et al. 2006). Our current result is in line with these previous studies. Moreover, we provide another example of how a difficult problem can be solved by a rather simple but nevertheless sufficiently accurate approximation.

In the experimental design applied in this study, outbound distance has been found to be the only cue the ants use to optimize their search patterns. As we have shown recently (Merkle and Wehner 2009a), they do make use of additional cues. However, these cues—which have not been identified to date—are only available under certain circumstances, for example, when ants travel on the same route to and from the nest or when the path integrator has led them to a location close to the nest entrance. Therefore, we consider the outbound distance as one fundamental parameter that shapes the basic search pattern. Although there might be other parameters that have yet to be revealed, we suggest that outbound distance is the most important factor of all cues identified to date to influence the systematic search behavior in desert ants.

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